The Sespedectinae, a New Subfamily of Hedgehog-like Insectivores

MICHAEL J. NOVACEK[1]

ABSTRACT

A new subfamily of erinaceomorph insectivorans, the Sespedectinae, is defined to include *Sespedectes, Proterixoides,* and the more dentally conservative *Crypholestes.* All three genera are confined to the middle Eocene of southern California. A new species of *Sespedectes, S. stocki,* from the San Onofre area (? Santiago Formation) of northern San Diego County is recognized on the basis of size parameters of the lower molars. Dental evidence favors the placement of sespedectines within the dormaaliids. The subfamily is distinguished from other dormaaliids by its large, complex P³, bunodont molar cusp pattern, and several other dental features. The bunodont molar construction of sespedectines is reminiscent of the European "amphilemurids." There is evidence to suggest, however, that some of the special similarities between these two groups were independently derived. Contrary to some theories, sespedectines are not erinaceids, nor are they hyopsodontid condylarths. In a classification that reflects the pattern of relationships preferred here, the Dormaaliidae comprises three subfamilies, the Dormaaliinae (including *Dormaalius, Macrocranion,* and the tribe Amphilemurini), the Scenopaginae (*Scenopagus* and *Ankylodon*), and the Sespedectinae.

INTRODUCTION

So little is known about Early Tertiary insectivores . . . that speculations on the origin and history of the group must be based largely on existing structures and conditions and consequently the distinguishing of palaeotelic from caenotelic or adaptive conditions confronts us at every turn. (Gregory, 1910, p. 287)

Erinaceomorph insectivorans played a crucial role in early attempts to develop a higher-level classification of placental mammals. Gregory (1910) claimed, for example, that these forms comprised an ancestral stock for many orders of mammals. This venerable notion much later fell prey to criticisms of insectivorans as archetypical placental ancestors (Van Valen, 1967; Novacek, 1982). Nevertheless, fossil erinaceomorphs show

[1] Chairman and Assistant Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

features that suggest potential relationships with a wide variety of mammalian taxa. It is widely acknowledged that the resolution of relationships within the Erinaceomorpha directly bears on the problems of monophyly and affinities for other insectivoran clades as well as putative fossil primates, condylarths, and carnivorans (Saban, 1958; Russell, 1964; Van Valen, 1967; Novacek, 1982).

Erinaceomorphs are also distinguished by a comparatively rich fossil record. These are among the most abundant mammals in Early Tertiary faunas of North America and Europe, an abundance more effectively sampled through the recent emphasis of washing and sorting of matrix for small fossil bones and teeth. In this sense, Gregory's (1910) above-quoted remarks on the miserable fossil record of insectivorans no longer seems appropriate. Yet Gregory's statement holds true for at least one aspect of this record. Most early fossil insectivorans are represented only by isolated teeth or partial jaws. The incomplete anatomical data promote a sketchy picture of homologous characters and taxic relationships. Living insectivorans provide the primary evidence for monophyletic groups. The fossils are often relegated to paraphyletic, "waste-basket" categories that have been associated with other mammalian taxa in virtually any fashion imaginable (see Van Valen, 1967, fig. 7).

It is worthwhile, then, to review the rapidly increasing list of fossil erinaceomorphs for meaningful groupings. Presumably, even the partial anatomical sampling represented by fossil teeth can be used as evidence for a predictive classification of monophyletic taxa. Such a classification was the aim of several recent reviews (Krishtalka, 1976; Novacek, 1982; Novacek, Bown and Schankler, 1985; Koenigswald and Storch, 1983). The purpose of this paper is to identify the relationships of two of the better represented, but more problematic, fossil erinaceomorphs, the Eocene genera *Sespedectes* and *Proterixoides*. This purpose requires a more explicit hypothesis of erinaceomorph relationships (fig. 9) than previously proposed.

Stock (1935) first described *Proterixoides* and *Sespedectes* from the Uintan (=middle-late Eocene) of the Sespe Hills area in southern California. Stock remarked on the resemblance and possible close affinity of *Proterixoides* to Tertiary erinaceids, a view supported by several authors (e.g., Butler, 1948; McKenna and Simpson, 1959). Subsequently, these genera suffered a fate similar to that noted above for many other early Tertiary insectivorans. They were dispatched to the confusing and dentally diverse Erinaceomorpha and their relationships were left unclarified. It has even been suggested (Russell, 1964; Russell, Louis, and Savage, 1975) that *Sespedectes* and *Proterixoides* are primitive hyopsodontid condylarths.

Many additional specimens of erinaceomorphs were recovered from middle Eocene assemblages of San Diego County in the early 1970s. These efforts, by field parties from U.C. Berkeley and San Diego State University, led to the description of a third taxon, *Crypholestes* (Novacek, 1976), that appeared closely related to *Sespedectes*. Unfortunately, much of the original material of *Proterixoides* and *Sespedectes* collected by Stock could not be relocated and further study of the taxa was abandoned.

Two subsequent developments made feasible a renewed consideration of the southern California Eocene "hedgehogs." Dr. David Golz relocated and carefully curated Stock's original collection (acquired from California Institute of Technology by the Natural History Museum of Los Angeles County). This allowed comparison of the large Sespe samples of *Sespedectes* and *Proterixoides* with additional material from the San Diego Eocene. Secondly, several recent revisions of erinaceomorph groupings (Russell, Louis, and Savage, 1975; Krishtalka, 1976; Bown and Schankler, 1982; Novacek, 1982; Gingerich, 1983; Koenigswald and Storch, 1983; Novacek, Bown, and Schankler, 1985) provide a general framework for comparisons of the southern California taxa and the basis for a more highly resolved classification of the Erinaceomorpha.

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ABBREVIATIONS

AW, anterior width
L, maximum anteroposterior length
PW, posterior width
W, maximum width
W-TAL, talonid width
W-TRI, trigonid width
C.V., coefficient of variation
M, arithmetic mean
N, number of observations (sample size)
O.R., observed range of variation
S.D., standard deviation

LACM, Los Angeles County Museum of Natural History
LACM (CIT), specimens or localities originally in the California Institute of Technology now housed in Los Angeles County Museum of Natural History
UCMP, University of California Museum of Paleontology, Berkeley

DENTAL TERMINOLOGY AND CRITERIA FOR MEASUREMENTS

Dental terms follow those given by Rich (1981) modified from Van Valen (1967).

All specimens were measured on an Ehrenreich Photo Optical "Shopscope." Measurements are in millimeters rounded off to the nearest one-hundredth of a millimeter. Orientations of cheek teeth for measurements follow those given in Novacek (1976).

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758
ORDER INSECTIVORA CUVIER, 1817
SUBORDER ERINACEOMORPHA GREGORY, 1910
FAMILY DORMAALIIDAE QUINET, 1964
SUBFAMILY SESPEDECTINAE, NEW

TYPE GENUS: *Sespedectes* Stock, 1935.
INCLUDED GENERA: *Proterixoides* Stock, 1935; *Crypholestes* Novacek, 1976.
DIAGNOSIS: Shares with the dormaaliids *Scenopagus, Ankylodon, Dormaalius,* and *Macrocranion* the following derived dental features: P_{1-2} reduced, single-rooted, peglike, or procumbent; P_4 premolariform (with large protoconid, small metaconid and paraconid, and short weakly basined or unbasined talonid with one or two minute cuspules); paraconids on M_{1-3} transverse, sharp, crestiform (but worn to a lophid appearance), and closely approximated to metaconids; trigonids on M_{1-3} distinctly canted anteriorly and anteroposteriorly compressed in occlusal view; P^4 with sweeping metastylar crest, vestigial or absent metacone, and weak posterolingual expansion of cingulum or hypocone; well-developed hypocone on M^{1-2}. Differs from above genera in having a P_3 with a well-developed protoconid and a short heel; a P^3 well developed and similar in structure to P^4 with a prominent metastylar crest, paracone, protocone and posterolingual cingulum; a marked inflation of molar cusps giving the crowns a "bunodont" appearance; and large swollen hypocones and distinct conules on upper molars. Differs from (primitive) erinaceids in the small and simple structure of P_{1-2} and P_4, more crestiform paraconids, more canted lower molar trigonids, less progressively reduced dimensions from M_1 to M_3, and less salient paraconid on M_1. Similar to "amphilemurids" (*Amphilemur, Pholidocercus, Alsaticopithecus, Gesneropithex*) in having bunodont crowns of cheek teeth but differs from this group in having large, double-rooted P_3 with expanded protoconid (small, procumbent, and single-rooted in "amphilemurids"), weaker paraconid on P_4, a well-developed P^3 similar to P^4 in morphology, a less symmetrical P^4 with a strong, posteriorly extended metastylar crest, and

more semirectangular and transverse upper molars (semiquadrate in amphilemurids) with stylar shelves and spurs (stylar shelves and para- and metastylar spurs greatly reduced or absent on M^{1-3} in "amphilemurids").

DISTRIBUTION: Middle–later Eocene (Uintan), southern California.

DISCUSSION: The distinctive features shared by the southern California Eocene dormaaliids warrant recognition of a separate subfamily for these taxa. *Sespedectes*, by far the best represented form, is designated the nominal genus for the group. *Crypholestes* is the most conservative sespedectine; *Proterixoides*, in some aspects, the most derived.

The above diagnosis clarifies the inclusion of sespedectines within the Dormaaliidae (see also Novacek, 1982) but distinguishes them from more generalized dental taxa (*Scenopagus*) or divergently specialized forms. Confusion is likely to arise with comparisons of "amphilemurids" (see Koenigswald and Storch, 1983) and sespedectines. The two groups share the distinctly bunodont crown pattern that is a departure from the more sectorial dentition of primitive erinaceomorphs. "Amphilemurids" are, however, like *Macrocranion* and unlike sespedectines in the small size of P^3_3, the more symmetrical structure of P^4, and the more quadrate outline of the upper molars. These comparisons suggest a possible close affinity with *Macrocranion*. Koenigswald and Storch (1983) excluded this and other close associations for "amphilemurids," but their conclusion rests mainly on the observation that "amphilemurids" are extremely specialized in cheek tooth and certain cranioskeletal features. In the reduction of P^1_3, *Macrocranion* and *Dormaalius* show a greater special similarity to amphilemurids than to other erinaceomorphs. Perhaps amphilemurids shared a close common ancestry with *Macrocranion* but diverged radically from an ancestor with a "*Macrocranion*-like" cheek tooth morphology. Under this scheme, the bunodont construction of the molar cusps was derived independently in "amphilemurids" and sespedectines.

These conclusions are based on detailed comparisons of sespedectines with an array of taxa that have been transferred to and fro among erinaceids, "adapisoricids," dormaaliids, primates, and hyopsodontid condy-

larths. Essential aspects of these comparisons are given below.

Genus *Sespedectes* Stock, 1935

TYPE SPECIES: *Sespedectes singularis* Stock, 1935.

INCLUDED SPECIES: *Sespedectes stocki*, new species.

DIAGNOSIS: Differs from *Proterixoides* in its significantly smaller size and in having a less excavated P_4 talonid basin; a more crestiform paraconid on M_{1-3}, a less semiquadrate outline of M_{1-3}; a relatively more transverse P^3 of closer structure to P^4; a less rounded, more "squared" lingual border of P^{3-4}; more bulbous molar cusps; a distinct metacrista on M^2, and a greatly expanded metaconule on M^{1-2}. Differs from *Crypholestes* in having less transverse, more anteroposteriorly lengthened upper molars (especially M^2); more bulbous molar cusps; greatly expanded metaconules on upper molars; less prominent labial spurs on M^{1-2}; weak or absent precingulum on M^{1-3}; more inflated hypocone on M^2; later retention of DP^4; and only one small cusp (rather than two) on the P_4 talonid.

DISTRIBUTION: Friars, Mission Valley Formations, San Diego. ? Santiago Formation, Camp San Onofre. Sespe Formation, Ventura County. Middle–later Eocene (Uintan) southern California.

DISCUSSION: *Sespedectes* is the most abundant insectivoran in the southern California Eocene. The genus is known only from dentitions but there are possibly associated skeletal remains from UCMP locality V-72088 at Camp San Onofre. Although remains of *Crypholestes* in the San Diego sequence are slightly more abundant than *Sespedectes* (Table 1 in Novacek and Lillegraven, 1979), the former genus is not known from the Camp San Onofre or Sespe localities (Novacek, 1976, Table 1).

INTRAGENERIC VARIATION: No distinct, qualitative morphological differences were detected among specimens of *Sespedectes* from San Diego, Sespe, and San Onofre localities. Nevertheless, the large sample referable to this genus permits an assessment of morphometric variation. Raw dental measurements (tables 1, 2, 3) were statistically

analyzed according to the following procedure.

Each isolated tooth or isolated jaw was treated as an individual. The alternative practice of testing only the minimum number of individuals (the greatest number of a particular tooth from only one side of the jaw) is, in this case, an underestimate of sample size. Right and left rami were never found in association or even in close proximity. Isolated teeth were widely scattered throughout a given sampling of rock. It is doubtful that a significant percentage of complementary teeth from opposite sides of the jaw represent the same individual.

Large samples of cheek teeth were recovered from the Camp San Onofre locality (UCMP V-72088) but samples from other localities were smaller. Thus, certain neighboring samples of the same formation were grouped. This grouping was straightforward in the case of the Sespe localities, as locality LACM (CIT) 180 accounted for a large percentage of *Sespedectes* from that region. Grouping was more problematical for the San Diego–Fletcher Hills localities, where sample sizes were much smaller. "Lumping" data in this manner increases sample size, but lessens the confidence of identifying homogeneous populations (Rensberger, 1971, p. 11). Nevertheless, lumped samples showed coefficients of variation that were generally close to 5 or 6 (Simpson, Roe, and Lewontin, 1960) and grouped samples showed variances often homogeneous with that of the large, normally distributed sample of V-72088. These results justify the organization of data used in this statistical comparison.

Only lower molars were recovered in sufficient numbers for comparison. Three samples were recognized: sample 1 comprised only UCMP V-72088 from Camp San Onofre (table 1); sample 2 included four proximate localities in the Mission Valley Formation exposed in the Fletcher Hills area of San Diego proper (UCMP V-6893, UCMP 6871, LACM 65190, UCMP V-71055) (table 2); sample 3 comprised four localities from the Sespe Formation in canyons of the Sespe Hills of Ventura County, California (LACM [CIT] 150, LACM [CIT] 180, LACM [CIT] 202, LACM [CIT] 207) (fig. 1, table 3).

It is likely that both samples 1 and 2 rep-

TABLE 1
Measurements of Cheek Teeth of *Sespedectes stocki* n. sp. from UCMP Locality V-72088 (San Onofre, ?Santiago Formation)

Symbols are defined under Abbreviations. All raw measurements are in millimeters.

Element and Dimensions		N.	O.R.	M.	S.D.	C.V.
P_3	L	10	1.33–1.82	1.50	0.125	8.4
	W	10	0.94–1.46	0.98	0.058	5.9
P_4	L	21	1.48–1.90	1.72	0.134	7.7
	W	19	1.04–1.35	1.19	0.100	8.0
M_1	L	20	1.47–2.03	1.79	0.139	7.8
	W-TRI	17	1.22–1.50	1.35	0.088	6.5
	W-TAL	17	1.19–1.48	1.36	0.095	7.1
M_2	L	28	1.50–1.86	1.72	0.114	6.6
	W-TRI	26	1.36–1.72	1.45	0.101	6.9
	W-TAL	27	1.23–1.54	1.41	0.086	6.1
M_3	L	13	1.67–1.82	1.72	0.099	5.8
	W-TRI	12	1.10–1.33	1.19	0.102	8.6
	W-TAL	11	0.95–1.10	1.01	0.050	5.0
P^3	L	4	1.73–1.84	1.78	0.041	2.3
	AW	4	1.62–1.69	1.65	0.024	1.4
	PW	4	1.50–1.81	1.63	0.113	6.9
P^4	L	8	1.46–1.84	1.65	0.123	7.4
	AW	9	1.57–2.17	2.02	0.131	6.4
	PW	8	1.57–2.09	1.90	0.156	8.2
M^1	L	4	1.69–1.85	1.73	0.068	3.9
	AW	4	2.00–2.26	2.16	0.096	4.4
	PW	5	2.27–2.49	2.32	0.080	3.4
M^2	L	4	1.46–1.87	1.66	0.183	11.0
	AW	4	2.00–2.30	2.13	0.122	5.7
	PW	4	1.80–2.15	1.97	0.132	6.7
M^3	L	5	1.05–1.42	1.29	0.129	9.9
	AW	5	1.37–1.72	1.53	0.127	8.3
	PW	5	1.06–1.39	1.29	0.125	9.6

resent rock sections more restricted temporally than sample 3. There was, however, no evidence of variation in tooth dimensions among samples of the Sespe Formation that could lead one to infer marked temporal change.

An "F max" test (Sokal and Rohlf, 1969, pp. 375–376) revealed that within-group variances of the three samples were homogeneous for all linear dimensions (antero-posterior length, trigonid width, talonid width). The null hypothesis that geographic location had no effect on tooth size was then tested. Results of a Student's T-test showed

TABLE 2

Measurements of Cheek Teeth of _Sespedectes singularis_ from UCMP V-6893, V-6871, V-71055, and LACM 65190 ("Fletcher Hills" Mission Valley Formation)

Symbols are defined under Abbreviations. Raw measurements are in millimeters.

Element and Dimensions		N.	O.R.	M.	S.D.	C.V.
P_3	L	1	1.40	—	—	—
	W	1	0.90	—	—	—
P_4	L	3	1.66–1.74	1.70	0.033	1.9
	W	4	0.82–1.20	1.08	0.152	14.0
M_1	L	8	1.58–1.97	1.74	0.170	9.7
	W-TRI	8	1.10–1.31	1.22	0.074	6.1
	W-TAL	8	1.10–1.31	1.24	0.071	5.7
M_2	L	7	1.52–1.90	1.69	0.151	8.9
	W-TRI	6	1.15–1.44	1.32	0.100	7.6
	W-TAL	7	1.14–1.34	1.26	0.104	8.3
M_3	L	6	1.50–1.68	1.60	0.064	4.0
	W-TRI	6	0.97–1.10	1.03	0.056	5.4
	W-TAL	6	0.80–0.90	0.86	0.031	3.6
P^3	L	3	1.57–1.74	1.72	0.041	2.3
	AW	2	1.72–1.77	1.65	0.024	1.4
	PW	2	1.74–1.90	1.63	0.113	6.9
P^4	L	3	1.56–1.72	1.66	0.075	4.5
	AW	3	2.22–2.41	2.29	0.081	3.5
	PW	3	2.11–2.25	2.16	0.065	3.1
M^1	L	4	1.64–1.83	1.67	0.156	9.3
	AW	4	1.85–2.25	2.07	0.146	7.1
	PW	4	1.82–2.50	2.26	0.264	11.7
M^2	L	3	1.65–1.74	1.68	0.040	2.4
	AW	3	2.15–2.20	2.16	0.023	1.1
	PW	3	2.04–2.07	2.05	0.012	0.6
M^3	L	2	1.15–1.18	1.17	0.015	1.2
	AW	2	1.56–1.74	1.65	0.090	5.5
	PW	2	1.25–1.28	1.27	0.015	1.2

TABLE 3

Measurements of Cheek Teeth of _Sespedectes singularis_ from Sespe Formation Localities LACM (CIT) 150, 180, 202, and 207

Dental dimensions and statistical parameters are defined under Abbreviations. Raw measurements are in millimeters.

Element and Dimensions		N.	O.R.	M.	S.D.	C.V.
P_3	L	4	1.41–1.67	1.59	0.120	7.6
	W	4	0.83–1.14	0.96	0.129	13.5
P_4	L	24	1.48–2.02	1.70	0.146	8.6
	W	24	0.88–1.58	1.12	0.145	13.1
M_1	L	30	1.53–2.12	1.78	0.165	9.3
	W-TRI	29	1.08–1.43	1.25	0.090	7.2
	W-TAL	30	1.12–1.55	1.32	0.116	8.8
M_2	L	34	1.42–2.10	1.71	0.143	8.4
	W-TRI	34	1.12–1.63	1.35	0.127	9.4
	W-TAL	34	1.02–1.55	1.30	0.117	9.0
M_3	L	6	1.46–1.88	1.61	0.163	10.1
	W-TRI	6	1.02–1.38	1.15	0.142	12.3
	W-TAL	6	0.77–1.11	0.93	0.129	13.9
P^3	L	1	1.41	—	—	—
	AW	1	1.94	—	—	—
	PW	1	1.94	—	—	—
P^4	L	1	—	—	—	—
	AW	1	2.22	—	—	—
	PW	1	2.28	—	—	—
M^1	L	5	1.50–1.95	1.74	0.198	11.4
	AW	5	1.96–2.25	2.14	0.109	5.1
	PW	5	2.16–2.47	2.31	0.125	5.4
M^2	L	8	1.38–1.81	1.60	0.143	8.9
	AW	8	2.09–2.37	2.16	0.976	4.1
	PW	8	1.65–2.18	2.00	0.056	7.8
M^3	L	1	1.16	—	—	—
	AW	1	1.74	—	—	—
	PW	1	1.18	—	—	—

that the null was rejected only in comparisons of trigonid width of M_1 between sample 1 and 2 and 1 and 3; talonid width of M_1 between 1 and 2; trigonid width of M_2 between 1 and 2 and 1 and 3; and talonid width of M_2 between 1 and 2 and 1 and 3 (table 4). In short, the San Onofre sample (inferred population) is distinctive in several molar dimensions from the Fletcher Hills and Sespe "populations."

These statistical results are corroborated by the observation that M_3s of _Sespedectes_

from UCMP V-72088 were relatively larger than M_3s of the same genus from other localities (fig. 1, A and B). In this case neither sample 2 nor 3 was large enough for statistical comparison with sample 1. Hence the former two samples were nested. This procedure is not intended for comparisons of inferred "local populations" but merely as a test of the apparent discreteness of M_3s from UCMP V-72088. Lumping samples 2 and 3 yielded CVs ranging between 4 and 6 for all dimensions of M_3. Combining these with sample 1
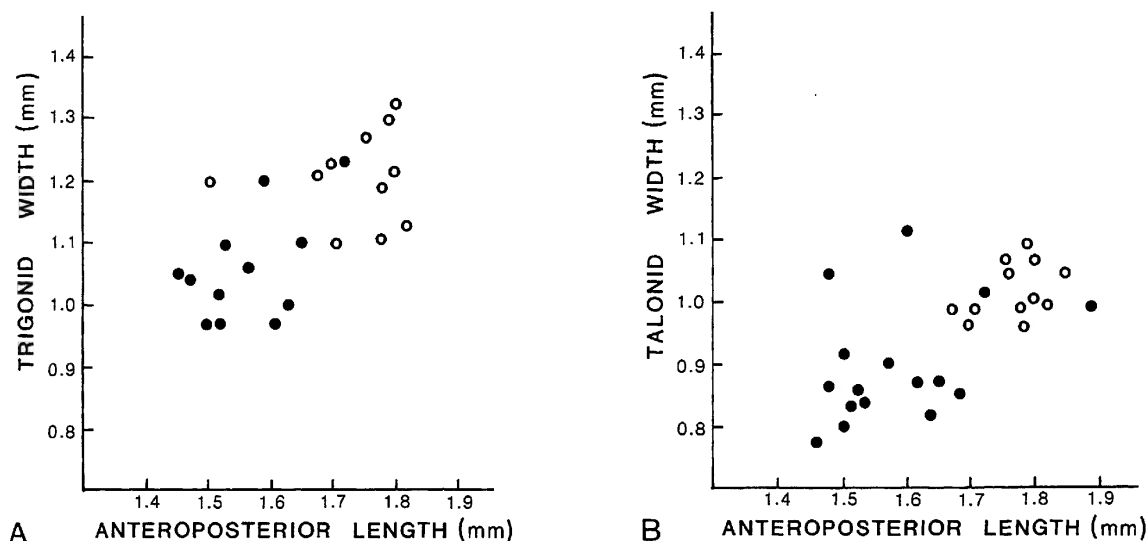
FIG. 1.   Plots of trigonid width (A) and talonid width (B) against anteroposterior length for M_3s of *Sespedectes*. Open circles, sample 1 (locality UCMP V-72088). Solid circles, combined samples 2 and 3 (localities UCMP V-6893, 6871, 71055, LACM 65190, LACM (CIT) 150, 180, 202, 207). See text for locality information.

yielded CVs greater than 7 and, in the case of trigonid width, as high as 11.

This indication of heterogeneity was supported by Student's T-test, which revealed significant differences between sample 1 and the nested samples 2 and 3 in all M_3 parameters. Scatter diagrams also show, albeit some overlap, a cluster of M_3 dimensions from the V-72088 sample that are clearly separated from M_3 dimensions of other samples (fig. 1).

What do these statistical comparisons mean for taxonomy? The debate over the nature of a fossil species reflects a desire to recognize something comparable to "reproductively isolated populations." Fossil taxa can only be identified by their structural characters and, as such, variation in these characters—morphological differences—must be taken seriously. The sample of *Sespedectes* from V-72088 is homogeneous, yet it is significantly different in size parameters of M_{1-3} from other samples. The individuals from the San Onofre locality are therefore recognized as a new species of *Sespedectes* (see diagnosis and discussion below).

Sespedectes singularis Stock, 1935

TYPE SPECIMEN: LACM (CIT) 1785, left mandible complete from anterior side of canine alveolus to slightly posterior of anterior

TABLE 4

Calculated t Values for Comparisons of M_1, M_2 Dimensions from Samples 1, 2, and 3 (see text and tables 1, 2, and 3, respectively) of *Sespedectes*[a]

Elements and Dimensions		Samples Compared	C.L.	t_{calc}	H_0
M_1	L	1-2	2.06	0.84	accepted
		1-3	2.01	0.22	accepted
		2-3	2.03	0.61	accepted
	W-TRI	1-2	2.07	3.86	rejected
		1-3	2.02	4.00	rejected
		2-3	2.03	0.87	accepted
	W-TAL	1-2	2.06	3.06	rejected
		1-3	2.01	1.22	accepted
		2-3	2.03	1.85	accepted
M_2	L	1-2	2.04	0.60	accepted
		1-3	2.00	0.30	accepted
		2-3	2.02	0.33	accepted
	W-TRI	1-2	2.04	2.45	rejected
		1-3	2.00	3.09	rejected
		2-3	2.02	0.54	accepted
	W-TAL	1-2	2.02	3.62	rejected
		1-3	2.00	4.02	rejected
		2-3	2.02	0.78	accepted

[a] C.L. is critical t value for rejection of the null hypothesis (H_0) that there is no significant difference between sample means, at P (level of significance) = 0.05 and DF (degrees of freedom) = N − 1. T_{calc} is calculated t value derived from sample means.

border of coronoid process, with P_3–M_3 (Stock, 1935, plate 1, figs. 6, 6a).

TYPE LOCALITY: LACM (CIT) 150, "Pearson Ranch," Brea Canyon Section, Sespe Formation. North of Simi Valley, Ventura County, California.

DIAGNOSIS: Differs from *Sespedectes stocki* in having slightly (but significantly) narrower trigonids and talonids on M_{1-2} and smaller M_3s (tables 1–4, fig. 1).

LOCALITIES AND REFERRED SPECIMENS: Locality LACM (CIT) 150. "Pearson Ranch," Sespe Formation between Brea and Alamos Canyons, Ventura County, California: mandible fragments with P_4–M_3, LACM 42628; P_4–M_2, LACM 42624; P_4–M_1, LACM 42627; M_{1-3}, LACM 42626; M_{1-2}, LACM 42625.

Locality LACM (CIT) 180. "Tapo Canyon," Sespe Formation, Ventura County, California: Mandible fragments with P_3–M_3, LACM (CIT) 1892; P_2–M_2, LACM (CIT) 1893; P_4–M_1, LACM 39970; M^3, LACM 39971, 39972, 39995, LACM (CIT) 5198, 5199; maxillary fragments with M^{1-2}, LACM 39982; M^{2-3}, LACM 39983; isolated P_4s, LACM 39969, 39976; isolated lower molars, LACM 39973–39975, 39977–39980, 39991–39995, 39997–39999, 40177, 40181, 40186, 40192; isolated upper molars, LACM 39984, 39985, 40189.

Locality LACM (CIT) 202. "Brea Canyon," Sespe Formation, Ventura County, California: Mandible fragments with P_3–M_3, LACM (CIT) 1433; P_4–M_3, LACM (CIT) 1891; P_4–M_2, LACM (CIT) 5197, 5200; P_4–M_1, LACM 37955, 37956, 37959, 37965, 42386; M_{1-3}, LACM (CIT) 5196; M_{1-2}, LACM 37958, 37967, 42388; M_{2-3}, 37960, 37994; maxillary fragments with M^{1-3}, LACM 37942; M^{1-2}, LACM 37943; M^{2-3}, LACM 37944; isolated P_4s, LACM 37957, 37964, 37969, 37993, 37995, 37996, 37998, 42387; isolated lower molars, LACM 37940, 37941, 37962, 37963, 37968, 37971, 37977–37985, 37987–37990, 37992, 42389; isolated P^4s, LACM 37954; isolated upper molars, LACM 37946–37953.

Locality LACM (CIT) 207. "Brea Canyon," approximately 75 ft stratigraphically below and 400 ft west of locality LACM (CIT) 202. Sespe Formation, Ventura County, California. Mandible fragment with P_4–M_3, LACM (CIT) 1890; maxillary fragment with P^1, P^3–M^3, LACM (CIT) 1889; P^4–M^2, LACM 42615; M^1, LACM 42616; M_2, LACM 42617; M^2, LACM 42618.

Locality UCMP V-6893. "Jack-in-the-Box," Fletcher Hills District. Mission Valley Formation, San Diego County, California. Mandible fragments with P_3–M_3, UCMP 95865; P_4–M_1, UCMP 96188; M_{1-2}, UCMP 96146; M_{1-3}, UCMP 96150; maxillary fragment with DP^3–M^2, UCMP 96161; P^4–M^3, UCMP 96151; P^{1-4}, UCMP 85681; isolated lower molars, UCMP 96125, 96143, 96177, 96162, 96434; isolated P^3, UCMP 96126; isolated upper molars, UCMP 96093.

Locality UCMP V-6871. "Fletcher Parkway." Fletcher Hills District. Mission Valley Formation, San Diego County, California. P_4, UCMP 101333; M^1, UCMP 99330. Several additional isolated teeth.

Locality LACM V-65190. "Fletcher Hills." Mission Valley Formation, San Diego County, California. Mandible fragments with P_4, M_{1-2}, UCMP 15955, 15959; M_{2-3}, UCMP 15956.

Locality UCMP V-71055. "Baltimore Locality." Fletcher Hills District, Mission Valley Formation, San Diego County, California. Maxillary fragments with P^{3-4}, UCMP 96158; M^{1-2}, UCMP 96144.

Locality UCMP V-6873. "Dog Spring Two" Mission Gorge. Friars Formation, San Diego County, California. M_1, UCMP 99341.

Locality UCMP V-68116. "Dog Spring Three" (Shrew Hill). Mission Gorge, Friars Formation, San Diego County, California. P^4s, UCMP 99367, 99123.

Locality UCMP V-71175. "Soiset's Surprise." Friars Formation, San Diego County, California. M_2, UCMP 96134.

DESCRIPTION: Other than the morphometric differences noted above, *Sespedectes singularis* and *S. stocki* are essentially identical. This description applies to both taxa. The mandible is slender, tapering anteriorly from a point below M_1. The masseteric fossa is bordered anteriorly by a prominent ridge. The coronoid process is high, and anteroposteriorly broad. The condyloid process is higher than the tooth row and is closer to the dorsal crest of the coronoid process than to the angular process. There is a horizontal ridge on the medial surface of the angular process, which curves slightly upward in its anterior
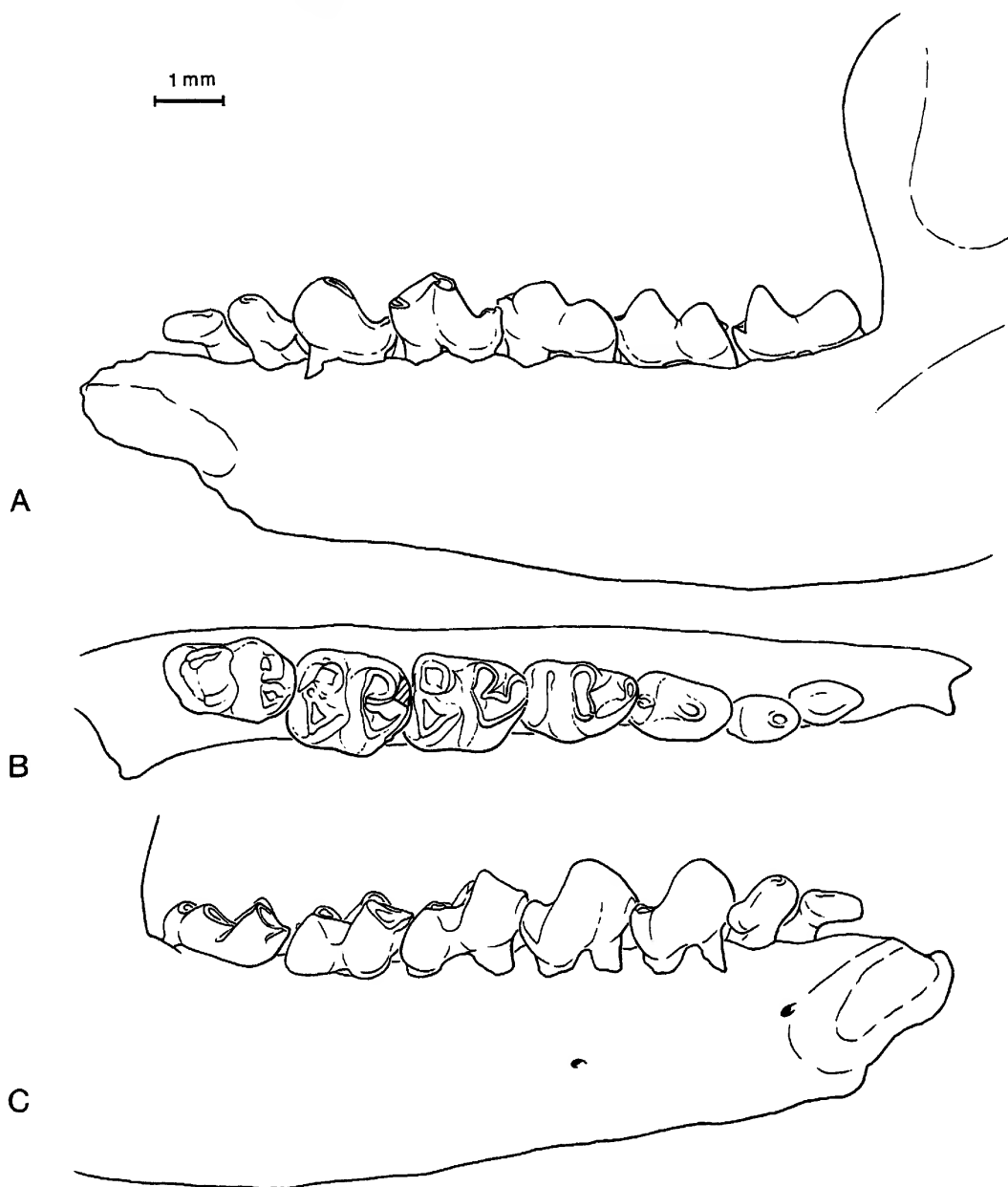
FIG. 2. *Sespedectes stocki*. (A) lingual; (B) occlusal; (C) labial views of UCMP 99391 (type), right mandible with P_1–M_3 from locality UCMP V-72088.

section. The inferior dental foramen (preserved in UCMP 96584) is located directly above the anterior section of the angular process about the level of the tooth row. The symphysis of the jaw terminates at a point below P_1. The anterior mental foramen is below P_2, the posterior mental foramen below the anterior root of P_4. All the teeth of the lower jaw, particularly the anterior premolars, are crowded.

None of the jaws was preserved with incisors, but roots and alveoli indicate that I_2 was enlarged and I_3 was much smaller. Isolated incisors from UCMP V-72088 have a mitten-shaped profile with long, transversely flattened roots. These are probably referable to *Sespedectes stocki* and are comparable to those of *S. singularis*.

Alveoli also indicate that the lower canine is single-rooted and not greatly enlarged.

P_{1-2} are not definitely known in *S. singularis,* but in *S. stocki* these teeth are procumbent, reduced, and single-rooted with a single, rounded cusp (fig. 2).

P_3 is double-rooted and, from comparisons with alveoli in *Sespedectes singularis* and known teeth in *S. stocki,* is much larger than P_1 and P_2. The crown is essentially a large, rounded cusp and a very small heel separated by a shallow trough. There is sometimes a minute cuspule on the transverse ridge of the posterior heel. Slightly lingual and anterior to this cuspule is an even smaller cuspule, discernible in slightly worn or unworn teeth. There is a shallow hypoflexid (fig. 2).

P_4 varies considerably in appearance with wear. In the type and in most other specimens this tooth is quite worn and the paralophid makes an unbroken descent from the apex of the protoconid. In unworn P_4s, the paralophid protrudes anteriorly in a rounded shoulder about midway down its length. The paraconid varies in form from a small, low cusp to a worn ridge representing the transverse spur of the paralophid. The metaconid is much lower than the protoconid and is situated labial and slightly posterior to it. The labial face of the metaconid coalesces with the protoconid for most of its height. A deep posteroventrally sloping trough separates the talonid ridge from the back of the protoconid and metaconid. The talonid is an oblique ridge with a single cusp often obscured by wear. The apices of the metaconid, protoconid, and the crest of the paralophid are often worn to a single, continuous wear facet (figs. 2, 5).

M_1 is slightly longer than wide with a low, anteriorly canted trigonid. The protoconid and metaconid are swollen at their bases and are subequal in height. A short paralophid curves anterolingually from the apex of the protoconid, terminating in a low paraconid. In unworn teeth, the paraconid is anteroposteriorly compressed, bladelike, and inclined forward. The paraconid is located directly anterior and labial to the metaconid. There is a short anterior cingulum. In most specimens, the talonid is slightly wider than the trigonid. The crista obliqua is a blunt ridge that contacts the post-vallid wall slightly labial to the protoconid-metaconid juncture. The hypoconid and entoconid are subequal in height and are much higher than the hy-

poconulid. The hypoconulid is not lingually positioned but is situated roughly midway between the hypoconid and entoconid and slightly posterior to them (figs. 2, 5).

Circular wear facets appear early on apices of all cusps of M_1 except the paraconid. On the latter, an elliptical wear facet develops which is continuous with that on the paralophid. Heavy wear on the protoconid usually precedes that on the metaconid. Late stages of wear show a confluent facet linking all trigonid cusps and connecting lophs. The sequence of wear is as follows: (1) circular wear facets on the three talonid cusps, (2) a confluent facet joining hypoconid and hypoconulid, (3) extensive wear on the hypoconulid and hypoconid until these cusps are worn level with the talonid basin, while the entoconid remains prominent and cuspate (a diagnostic erinaceomorph wear pattern), (4) extensive wear of the entoconid and confluent facets joining all three cusps.

M_2 is similar in structure and wear pattern to M_1 except that it is relatively wider with a talonid slightly narrower than the trigonid and a smaller paraconid less separated from the metaconid.

M_3 is smaller than M_{1-2} with a much narrower and more elongate talonid. Unlike M_{1-2} the hypoconulid is a prominent, more posteriorly and lingually positioned cusp. Wear on the hypoconid precedes that on the hypoconulid and entoconid. In later stages of wear the latter two cusps form a distinct crest with a confluence of their steep lingual faces.

Maxillary fragments rarely preserve teeth anterior to P^3. An upper canine is unknown in *Sespedectes singularis,* but this tooth in *S. stocki* is small and single-rooted with a button-shaped crown that resembles P^{1-2} (fig. 4A).

The latter teeth are preserved in UCMP 85681 (from UCMP V-6893). They are single-rooted and essentially identical in appearance. P^1 is slightly smaller than both C and P^2 (fig. 3, A, B, and C).

The three-rooted DP^3 is much longer than wide (fig. 3E). Its principal feature is a high paracone. Sloping posterolabially from the paracone is a distinct crest that lacks a metacone. The labial face of the paracone is flat and steep; the lingual face, more gently sloping. There is no distinct stylar shelf. The parastylar spur is prominent and rounded in oc-
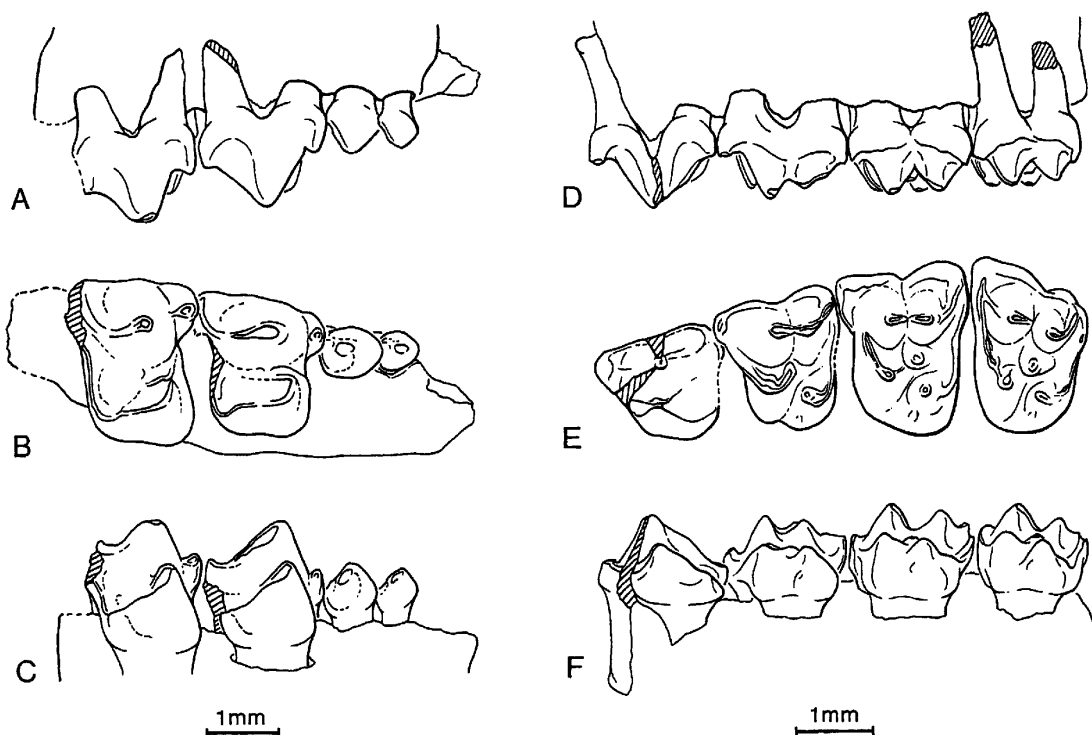
FIG. 3. *Sespedectes singularis*. (A) labial; (B) occlusal; (C) lingual views of UCMP 85681, right P$^{1-4}$. (D) labial; (E) occlusal; (F) lingual views of UCMP 96161, DP$^{3-4}$, M$^{1-2}$. Both specimens from locality UCMP V-6893.

clusal view and is developed into a small, bulbous cusp (parastyle). The protocone is much lower than the paracone. Its posterior face is worn to a flattened slope inclined at about 45° (fig. 3F) to the horizontal plane of the tooth row. A swelling in the posterolingual corner of the crown suggests the presence of a low, weak hypocone (fig. 3).

DP^4 is molariform and is more transverse than DP^3; its posterior width is nearly equal to its anteroposterior length. Both a paracone and metacone are present, the latter being lower than the former. The paracone of DP^4 is significantly lower than the paracone of DP^3 and the latter seems to have functioned as a puncturing cusp similar to posterior premolar paracones of more modern erinaceids. A weak metacrista is present and protrudes slightly beyond the labial margin of the more anterior section of the crown. As in DP^3 there is no appreciable stylar shelf and the protocone is much lower than the paracone. The preprotocrista extends to the parastyle. The hypocone is well developed and situated more lingually than the higher protocone. It is sep-

arated from the wall of postprotocrista by a shallow trough. There is a distinct metaconule but no paraconule. A precingulum is absent. As in DP^3, the lingual root is anteroposteriorly broader than the labial roots (fig. 3, D, E, and F).

The three-rooted P^3 is slightly wider than long with a high, triangular (in labial view) paracone. There is a strong, sweeping metastylar crest but no evidence of a metacone. There is a minute parastyle opposite the anterolabial corner of the paracone which projects slightly beyond the straight, anterior margin of the crown. The labial margin is slightly convex opposite the paracone. There is no appreciable stylar shelf. The low protocone is bordered posteriorly by a weak bulge that may be a hypocone. The posterior face of the protocone tends to wear to an inclined slope similar to that in DP^3 (figs. 3, 4, 5, 8).

P^4 is essentially identical to P^3 in structure, differing only in its slightly larger size and more transverse proportions, a more oblique anterior margin, and a more prominently projecting parastyle (figs. 3, 4, 5, 8).
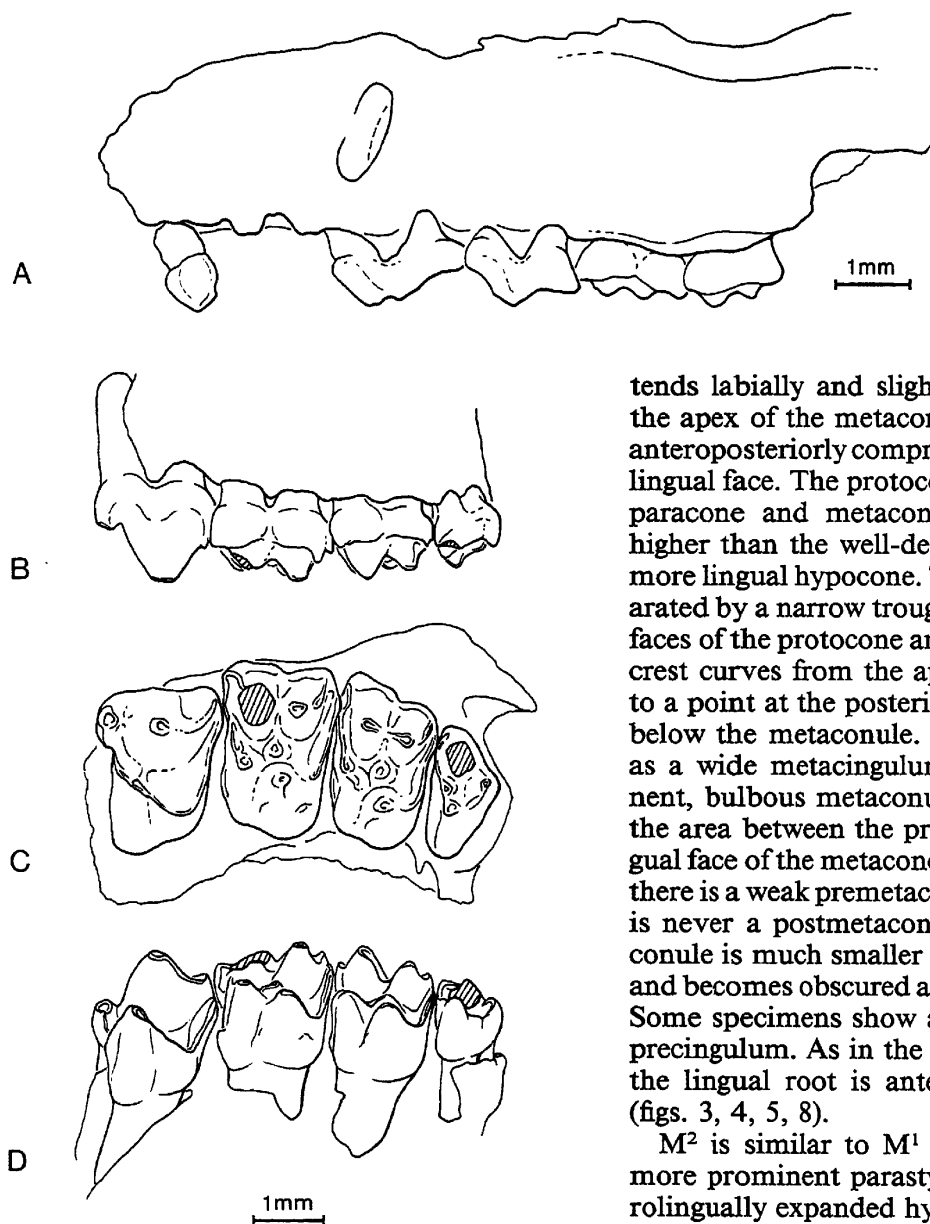
FIG. 4. *Sespedectes stocki.* (A) lateral view of UCMP 99401, right maxilla with C, P³⁻⁴, M¹⁻² (image reversed) from locality UCMP V-72088. *Sespedectes singularis.* (B) labial; (C) occlusal; (D) lingual views of 96151, left P⁴, M¹⁻³ from locality UCMP V-6893.

M¹ is rectangular to semiquadrate with its length equal to or greater than three-fourths its width. There is a weak ectoflexus and stylar shelf. All the molar cusps are low and rather bulbous in construction. The paracone and the metacone are well separated and are subequal in height. The strong metacrista ex-

tends labially and slightly posteriorly from the apex of the metacone. The protocone is anteroposteriorly compressed with a rounded lingual face. The protocone is lower than the paracone and metacone and only slightly higher than the well-developed and slightly more lingual hypocone. The hypocone is separated by a narrow trough from the posterior faces of the protocone and postprotocrista. A crest curves from the apex of the hypocone to a point at the posterior base of the crown below the metaconule. It continues labially as a wide metacingulum. The very prominent, bulbous metaconule occupies most of the area between the protocone and the lingual face of the metacone. In some specimens there is a weak premetaconule wing, but there is never a postmetaconule wing. The paraconule is much smaller than the metaconule and becomes obscured at early stages of wear. Some specimens show a short, very narrow precingulum. As in the posterior premolars, the lingual root is anteroposteriorly broad (figs. 3, 4, 5, 8).

M² is similar to M¹ except for its much more prominent parastylar spur, less posterolingually expanded hypocone, and slightly lower more lingually positioned metacone. No M² shows a precingulum (figs. 3, 4, 8).

M³ is much smaller than M¹⁻², with a strong oblique labial margin and a very prominent parastylar spur. There is no metastylar lobe; the metacone occupies the extreme posterolabial corner of the crown. The paracone is much higher than the protocone and both cusps are higher than the metacone. The preprotocrista extends to the parastylar spur, forming a narrow cingulum along the anterior base of the paracone. Some specimens show a very small precingulum and postcingulum. The lingual root of M³ is not anteroposteriorly broadened as in M¹⁻² (figs. 4, 5, 8).
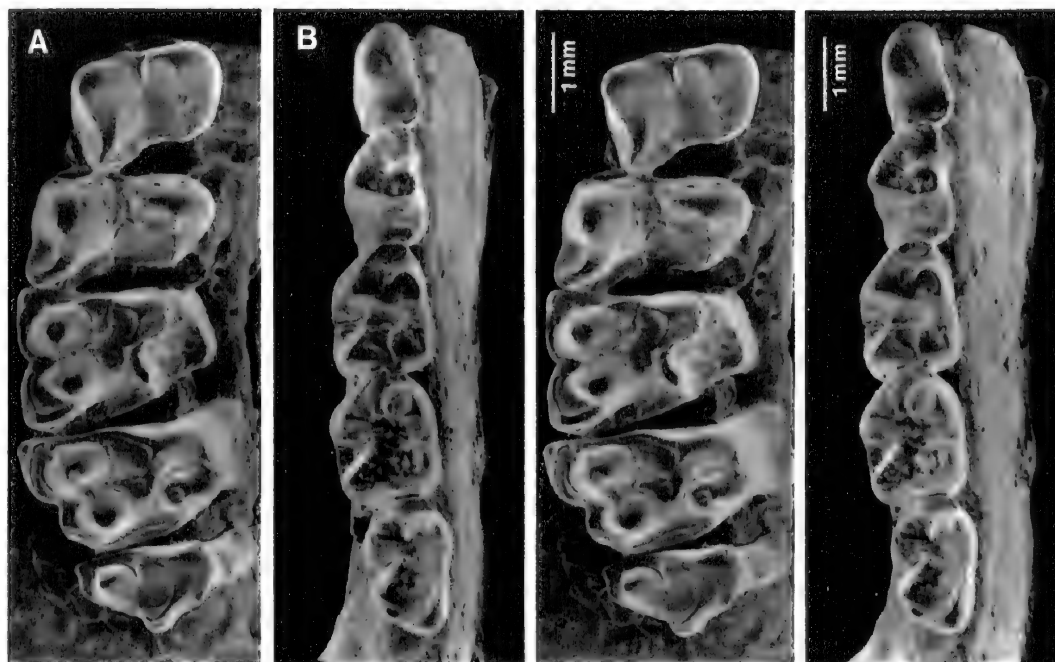
FIG. 5. Scanning electron stereomicrographs (occlusal views) of (A) *Sespedectes singularis*, LACM (CIT) 1889, right P^{3-4}, M^{1-3} from locality LACM (CIT) 207. (B) *Sespedectes stocki*, UCMP 99353, left P_{3-4}, M_{1-3} from UCMP V-72088.

Nothing is known of the skull of *Sespedectes singularis* aside from a few partial maxillary fragments associated with the upper dentitions described above. In these specimens the large anterior opening of the infraorbital canal is located above a point on the alveolar border between the labial roots of P^3 (fig. 4A). The anterior "root" of the zygoma begins at the level of M^1. The anterolateral surface of the zygomatic arch is strongly concave.

DISCUSSION: *Sespedectes singularis* co-occurs with *Crypholestes vaughni* in certain San Diego localities (Novacek, 1976, table 1; Golz and Lillegraven, 1977, table 1). The two species differ distinctly in upper molar structure (fig. 8), but not in size or morphology of the lower cheek teeth. The P_4 talonid of *C. vaughni* is bicuspid rather than unicuspid as in *S. singlularis*, but other differences between lower teeth are few and subtle. Isolated lower molars from some of these problematic localities (e.g., UCMP V-6873) are not included in the measurement analysis of *Sespedectes*.

Sespedectes but not *Crypholestes* is present in the Fletcher Hills localities of the Mission Valley Formation, while the latter alone is present in Poway localities north of San Diego, representing the same formation. Both species, as noted above, coexist in localities between these two areas which represent Friars and Mission Valley facies. All other things being equal—namely approximate time, elevation, and habitat—it is conceivable that this is an example of contiguous to slightly overlapping ranges of two closely related species. However, the equality of the properties mentioned has not been established.

An interesting difference between *Crypholestes* and *Sespedectes* relates to the ontogeny of tooth replacement. In the latter the eruption of the characteristic trenchant P^4 of erinaceomorphs is delayed, whereas *Crypholestes* exhibits the more typical pattern of an earlier replacement. Thus it is inferred that *Sespedectes* retained for a prolonged period a more extensive "crushing battery" comprising DP^{3-4}, M^{1-3} (Novacek, 1976, p. 24).

Sespedectes stocki, new species

ETYMOLOGY: Named after the late Chester Stock, who provided the original descriptions
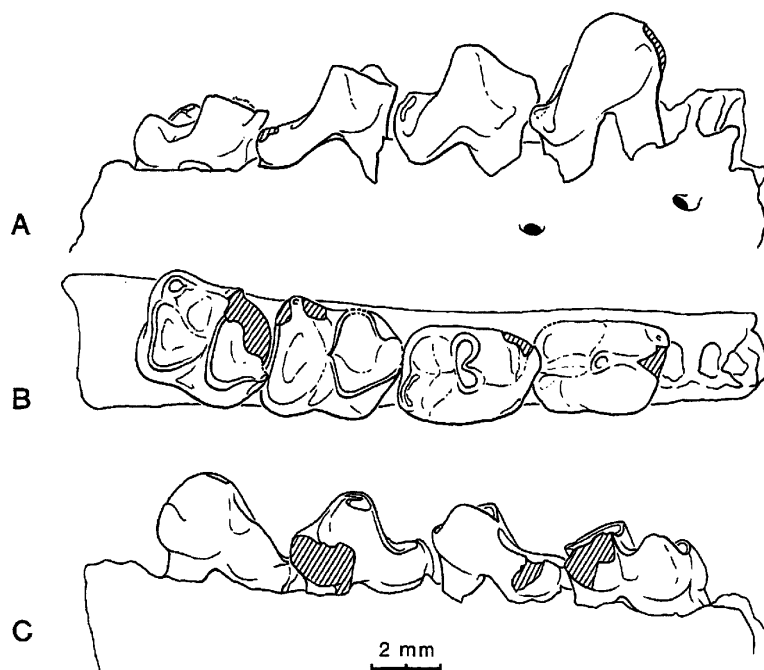
FIG. 6. *Proterixoides davisi.* (A) labial; (B) occlusal; (C) lingual views of LACM (CIT) 42594, right mandible with P_{3-4}, M_{1-2} from locality LACM (CIT) 150E.

of insectivores and many other mammals of the southern California Eocene.

TYPE SPECIMEN: UCMP 99391, right mandible with P_1–M_3 (fig. 2).

TYPE LOCALITY: UCMP V-72088 "Onofre Locality One." Sandstone lens near northern extreme of Camp Pendleton Marine Corps Base at Camp San Onofre. ?Santiago Formation, northwest corner of San Diego County. Possibly significantly younger than the Friars–Mission Valley Formation assemblage of greater San Diego and roughly equivalent to older parts (Tapo and Brea Canyon) of the Sespe Formation in Ventura County (Golz, 1976; Golz and Lillegraven, 1977).

DIAGNOSIS: Differs from *Sespedectes singularis* in having wider talonids and trigonids on M_{1-2} and larger, broader M_3s (tables 1–4, fig. 1).

LOCALITY AND REFERRED SPECIMENS (partial listing): All referable specimens from the type locality: Fragments of mandible with P_3–M_3, UCMP 98654, 99353; P_{3-4}, M_2, UCMP 99411, P_4–M_3, UCMP 98655, 98656, 99394, 99399; P_4–M_2, UCMP 101406; P_4–M_1, UCMP 98653, 99407, 101329; M_{1-2}, UCMP 99402, 99409, 99412, 101371; M_{2-3}, UCMP 98652, 99406, 99408, 99413, 99470; maxillary fragment with C, P^3–M^2, UCMP 99401;

M^{1-3}, UCMP 96461; isolated I_2s ?, UCMP 99452, 99492, 101341, 101353, 101391; I_3s ?, UCMP 99286, 99493, 101348, 101374, 101402; P_3s, UCMP 99361, 99396, 101363, 101365, 101400, 101405; P_4s, UCMP 99279, 99345, 99392, 99473, 101368, 101380, 101394; M_1s, UCMP 99404, 99416, 99472, 99656, 101349, 101387, 101390, 101395, 101406; M_2s, UCMP 98656, 99326, 99393, 99395, 99403, 99412, 99479, 101340, 101346, 101347, 101361, 101369, 101371, 101406; M_3s, UCMP 99275, 99353, 101372, 101376; P^3s, UCMP 99398, 99474, 101415; P^4s, UCMP 99355, 99397, 101350, 101351, 101356, 101357, 101381, 101408; M^1s, UCMP 99469, 101384, 101392; M^3s, UCMP 99490, 101377, 101383, 101385.

DISCUSSION: *Sespedectes* has also been reported from UCMP V-6883 ("Half-Day Pocket") and LACM 68102 ("Laguna Riviera Quarry") in the Santiago Formation near Carlsbad, California (Golz and Lillegraven, 1977, table 1). Specimens were tentatively assigned to *S. singularis,* but reference to *S. stocki* may be more appropriate. The Laguna Riviera material is currently under study by workers at the LACM, UCMP, and U.C. Riverside.

The San Onofre locality shows a curious
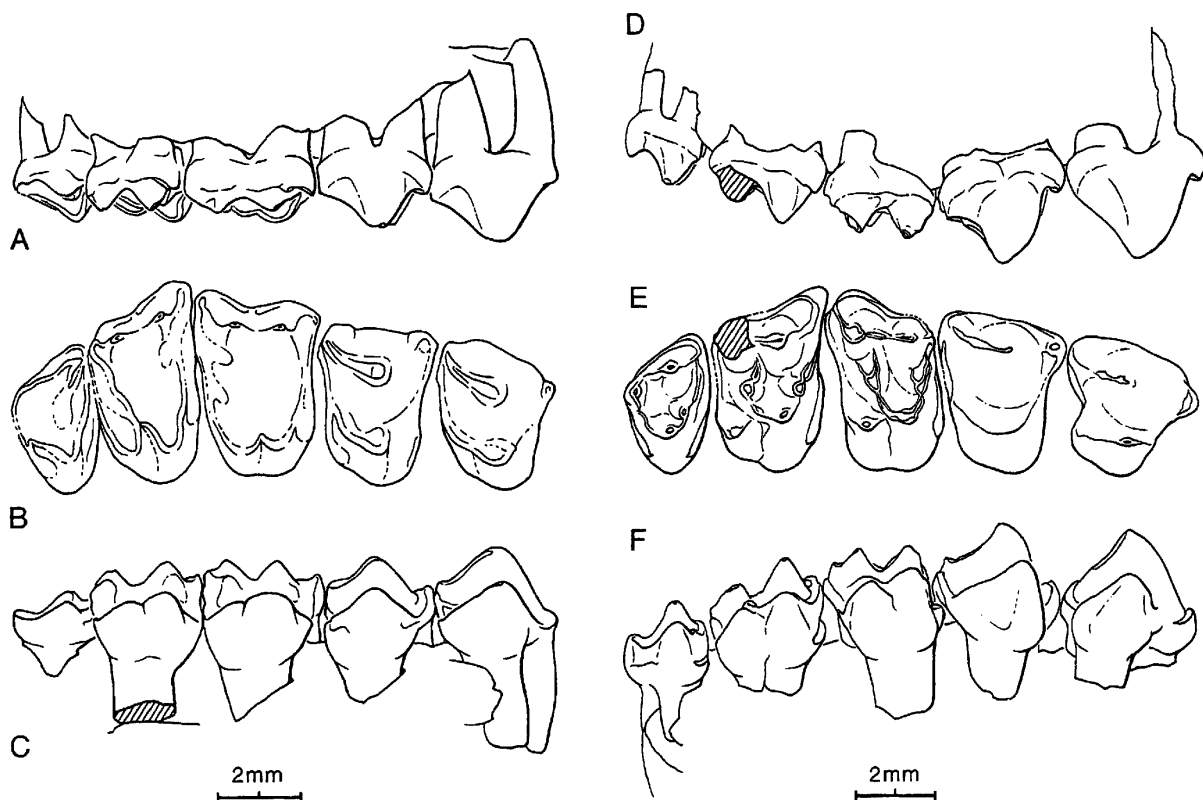
FIG. 7. *Proterixoides davisi.* (A) labial; (B) occlusal; (C) lingual views of LACM (CIT) 1674, left maxilla with P$^{3-4}$, M$^{1-2}$ (image reversed) from locality LACM (CIT) 150. (D) labial; (E) occlusal; (F) lingual views of LACM (CIT) 1873, right maxilla with P$^{3-4}$, M$^{1-3}$ from locality LACM (CIT) 150.

dominance of diversity by two taxa, *Sespedectes stocki* and the rodent *Simimys simplex.* Other San Diego County localities generally show more even relative abundances of several small insectivorans and rodents. The composition of the San Onofre sample may be influenced by certain taphonomic and sedimentary factors discussed in Novacek (1976, pp. 3–7).

Genus *Proterixoides* Stock, 1935

TYPE AND ONLY SPECIES: *Proterixoides davisi* Stock, 1935.

DIAGNOSIS: Differs from *Sespedectes* in its much larger size and in having a more excavated P$_4$ talonid basin; more lophid, rather than crestiform, paraconid on M$_{1-3}$, more quadrate outline of M$_{1-3}$; a less transverse, more triangular P^3 that is similar but does not match P^4 in outline and construction; a more evenly convex outline of the lingual

border of P$^{3-4}$; more conical, slightly less bulbous molar cusps; very weak or no metacrista on M^2; a less inflated metaconule on M^2. Differs from *Crypholestes* in being much larger and in having more quadrate upper molars and more swollen molar cusps (tables 5, 6; figs. 6, 7).

DISTRIBUTION: Sespe, ?Santiago, and Friars Formations, southern California. Uintan (middle–later Eocene).

Proterixoides davisi Stock, 1935

TYPE SPECIMEN: LACM (CIT) 1673, right maxillary fragment with P^3–M^2 (Stock, 1935, plate 1, fig. 1).

TYPE LOCALITY: LACM (CIT) 150 "Pearson Ranch," Brea Canyon Section, Sespe Formation. North of Simi Valley, Ventura County, California.

DIAGNOSIS: Same as for genus.

LOCALITIES AND REFERRED SPECIMENS (localities are described under listing for *Ses-*

TABLE 5

Measurements of Cheek Teeth of *Proterixoides davisi* from LACM (CIT) 150, 150E, 180, 202, and 207 (Sespe Hills, Sespe Formation)

Symbols are defined under Abbreviations. Measurements are in millimeters.

Element and Dimensions		N.	O.R.	M.	S.D.	C.V.
P_3	L	6	3.16–3.96	3.54	0.347	9.8
	W	6	1.82–2.27	2.40	0.401	16.7
P_4	L	21	2.95–4.19	3.68	0.349	9.5
	W	21	2.04–2.84	2.45	0.230	9.4
M_1	L	23	2.95–4.16	3.35	0.281	8.4
	W-TRI	23	2.16–3.11	2.55	0.218	8.5
	W-TAL	23	2.32–3.38	2.69	0.051	9.1
M_2	L	19	3.02–3.96	3.30	0.246	7.4
	W-TRI	19	2.51–3.29	2.75	0.188	6.8
	W-TAL	19	2.37–3.07	2.60	0.170	6.6
M_3	L	8	3.20–3.69	3.41	0.166	4.9
	W-TRI	8	2.08–2.43	2.25	0.124	5.5
	W-TAL	8	1.65–2.07	1.86	0.151	8.1
P^3	L	3	3.39–3.65	3.56	0.145	4.1
	AW	3	2.84–2.97	2.88	0.072	2.5
	PW	3	3.17–3.25	3.22	0.044	1.4
P^4	L	6	3.03–3.40	3.26	0.144	4.4
	AW	6	3.52–4.16	3.79	0.263	6.9
	PW	6	3.77–4.27	4.00	0.218	5.4
M^1	L	2	3.13–3.38	3.26	0.177	5.4
	AW	2	3.65–4.47	4.06	0.580	14.3
	PW	2	4.38–4.92	4.65	0.382	8.2
M^2	L	5	2.92–3.36	3.22	0.173	5.4
	AW	5	4.16–5.15	4.71	0.389	8.3
	PW	5	3.54–4.37	4.10	0.244	8.4
M^3	L	2	2.20–2.43	2.32	0.163	7.0
	AW	2	3.57–3.78	3.68	0.148	4.0
	PW	2	2.55–2.98	2.77	0.304	11.0

TABLE 6

Measurements of Cheek Teeth of *Proterixoides davisi* from San Diego County Localities UCMP V-68116 and V-72088

Symbols are defined under Abbreviations. Measurements are in millimeters.

Element	L	W-TRI	W-TAL
M_1 (UCMP 106078)	3.33	2.48	2.56
M_2 (UCMP 106078)	3.18	2.54	2.44
M_2 (UCMP 101335)	3.2^a	2.5^a	2.4^a

Element	L	AW	PW
P^4 (UCMP 101690)	2.9^a	3.12	3.4^a
M^1 (UCMP 99363)	3.1^a	–	–

^{a} Damaged specimen.

M_{2-3}, LACM 42595, isolated lower molars, LACM 42598.

Locality LACM (CIT) 180. "Tapo Canyon." Mandible fragments with P_3–M_1, LACM 39939; P_{3-4}, LACM 39938; P_4–M_1, LACM (CIT) 1886; P_4–M_2, LACM (CIT) 1887; M_{2-3}, LACM (CIT) 1874, 1888; maxillary fragments P^3–M^3, LACM (CIT) 1873; isolated P_3s, LACM 39936, 39937, 39964; P_4s, LACM 39940–39945, 39965–39967; lower molars, LACM 39946–39963, 39968; P^3s, LACM 39920, 39922; P^4s, LACM 39921; upper molars, LACM 39924–39935.

Locality LACM (CIT) 202. "Brea Canyon." Mandible fragment with P_4–M_1, LACM (CIT) 1885; P^4, LACM 37939.

Locality LACM (CIT) 207. "Brea Canyon." Mandible fragment with P_3–M_2, LACM (CIT) 1883; P_4–M_2, LACM 42607; P_3–M_1, LACM 42612; M_{2-3}, LACM (CIT) 1884, LACM 42608; P_3, LACM 42613; P_4, LACM 43614; lower molars, LACM 42609–42611; upper molars (M^2s), LACM 42605–42606.

Locality UCMP V-72088. "San Onofre" and Locality UCMP V-68116 "Dog Spring Three." Mandible fragment with M_{1-2}, UCMP 106078; M_2, UCMP 101335; P^4, UCMP 101690; M^1, UCMP 99363.

DESCRIPTION: Stock (1935) provided a brief, comparative description of this taxon. The features of *Sespedectes singularis* generally apply for *Proterixoides davisi* with the obvious exception of diagnostic differences specified above. Unfortunately, the anterior dentition is very poorly known in *Proterixoides*.

pedectes singularis): Locality LACM (CIT) 150, type locality. Mandible fragments with P_{3-4}, LACM 42602; P_4–M_3, LACM 42599; P_4–M_1, LACM 42620; M_{1-3}, LACM (CIT) 1677 (Stock, 1935; plate 1, fig. 2); M_{1-2}, LACM 42600; maxillary fragments with P^3–M^3, LACM (CIT) 1674; P^4, M^{2-3}, LACM (CIT) 1675 (Stock, 1935; plate 1, fig. 3); isolated lower molars, LACM 42601, 42603; P_4s, LACM 42603, 42621; P^4s, LACM 42622.

Locality LACM (CIT) 150E. "Pearson Ranch." Mandible fragments with P_3–M_2, LACM (CIT) 1678, LACM 42594; M_{1-2}, LACM 42596; M_{1-3}, LACM 42593, 42597;

DISCUSSION: Stock (1935, p. 218) reported that *Sespedectes singularis* was less abundant in CIT 150 collections than *Proterixoides davisi* but he did not publish sample sizes for either species. The relatively large samples of *Proterixoides* from the Sespe localities show high variation in certain tooth dimensions (e.g., P_4 length, width; M_1 talonid width; M^1 anterior width; M^3 posterior width; see table 5). Some of these parameters are difficult to measure with consistency (upper molar widths), and a large sample of M_2s shows low coefficients of variation for all parameters measured (table 5). If heterogeneity is present, there is no obvious pattern for it. Thus, all Sespe samples are referred to one species, *Proterixoides davisi.*

A small number of isolated teeth from the Santiago and Friars Formation of San Diego County are morphologically indistinguishable from the Sespe specimens. Measurements of these teeth fall within the range represented by the Sespe samples (table 6).

Genus *Crypholestes* (Novacek, 1976)
Novacek, 1980

TYPE AND ONLY SPECIES: *Crypholestes vaughni* Novacek, 1976.

DIAGNOSIS: Significantly smaller than *Proterixoides* with more transverse molars and less bulbous cusps. Very close in size and lower molar structure to *Sespedectes* but differs in having a bicuspid P_4 talonid; more transverse upper molars with more conical, less bulbous cusps; more prominent labial spurs (particularly parastylar spur of M^2); a consistently present precingulum on M^{1-3}; less swollen hypocone on M^2; labial extension of the postmetaconule wing as a metacingulum on M^{1-2}; DP^4 heavily worn at the time the molars are erupted (fig. 8B).

DISTRIBUTION: Friars, Mission Valley and ? Santiago Formations, San Diego County, California. Uintan (middle–later Eocene).

DISCUSSION: Detailed description of *Crypholestes* was provided elsewhere (Novacek, 1976), but this systematic review prompts a revised diagnosis. *Crypholestes* is dentally the least specialized member of the Sespedectinae. The genus, represented only by *C. vaughni,* is not known from the Sespe or other areas outside of the San Diego County Eocene.
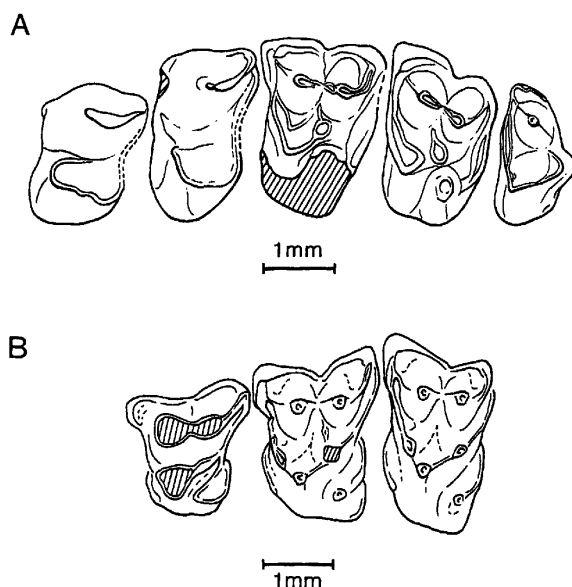
FIG. 8.   Comparisons of occlusal views of (A) *Sespedectes singularis,* LACM (CIT) 1889, right P^{3-4}, M^{1-3} (image reversed) from locality LACM (CIT) 207 and (B) *Crypholestes vaughni,* UCMP 103912, left P^4, M^{1-2} from locality UCMP V-71211.

RELATIONSHIPS OF THE SESPEDECTINAE

The bunodont appearance of the cheek teeth in sespedectines has been the source of some confusion. Russell (1964) and Russell, Louis, and Savage (1975) have suggested, for example, that these southern California taxa, at least *Proterixoides,* are possibly primitive hyopsodontid condylarths rather than erinaceomorphs. This claim can be disputed on several grounds.

First, hyopsodontids are so poorly defined that any small mammal with a rather generalized, nonsectorial dentition may find itself dispatched to this group. Nevertheless, Gingerich (1983) has recently provided some cogent arguments for distinguishing primitive erinaceomorphs from primitive hyopsodontids. In contrast to the latter, erinaceomorphs typically have sharper-cusped cheek teeth, a strong postmetacrista on P^4, M^{1-3}, more crestiform paraconids, and lack distinct labial cingula on the lower molars.

This demarcation, though generally useful, does not clearly establish the more bunodont *Proterixoides, Sespedectes,* and "amphilemurids" as erinaceomorphs. For this purpose,

additional characters are needed. Unlike hyopsodontids, these taxa have single-rooted, crowded anterior premolars; P_4s with weaker metaconids and short talonids with only small basins and cusps. (The P_4 talonid is generally large with a distinct basin in Hyopsodontinae, but reduced in the Mioclaeninae. The latter subfamily is, however, easily distinguished from *Proterixoides, Sespedectes,* and amphilemurids.) M_1 paraconids, though small and lophid in construction, are more salient; upper P^4 has a strong, sweeping metastylar crest typical of "modern" erinaceids, and the upper molars have stronger labial spurs, less inflated paracones, and more strongly developed hypocones.

These comparisons are discrepant with Russell's (1964) association of *Proterixoides* (and *Sespedectes*) and *Pascatherium dolloi* as closely related members of the Hyopsodontidae. Russell, Louis, and Savage (1975) excluded *Pascatherium* from Erinaceomorpha because of its double-rooted premolars, bunodont molars, vestigial or absent paraconids, mental foramen below or slightly anterior to M_1, and the lack of a postmetaconule crista. Only the last condition and the bunodont "gestalt" of the molars are shared with *Proterixoides* and *Sespedectes.* Moreover, variation in metaconule development is seen among generally similar upper molars of *Sespedectes, Proterixoides,* and *Crypholestes.* Only in *Sespedectes* is the development of a postmetaconule crest completely obscured by inflation of the metaconule (fig. 4). To sum, sespedectines show diagnostic erinaceomorph traits lacking in *Pascatherium* and more typical hyopsodontids.

The inclusion of sespedectines within Erinaceomorpha still leaves open several possibilities for relationships. These reflect interpretations in the literature that date back to Stock (1935). Sespedectines might qualify as erinaceids or "amphilemurids," or specialized dormaaliids, or a fourth clade of Erinaceomorpha separate from these groups. The alternatives will be briefly considered.

Stock (1935) regarded both *Proterixoides* and *Sespedectes* as erinaceids and noted the affinity of the former with the Oligocene genus *Proterix.* Butler (1948) in his comprehensive review of the Erinaceidae suggested that *Proterixoides* might have been an early

offshoot of the Erinaceinae while also being "transitional" between dentally more primitive galericines (= echinosoricines) and *Proterix.*

How valid are these associations? Table 7 summarizes dental comparisons of sespedectines with Recent Erinaceinae and Galericinae. In most features, sespedectines seem more primitive. Notably lacking in sespedectines are the marked elongation of the M_1, the progressive reduction in size from M_1 to M_3, the crest linking the hypocone with the postprotocrista, and the more quadrate dimensions of the upper molars—features which clearly define erinaceids.

The well-developed P^3 in sespedectines (character 13) is of phylogenetic interest. Most early erinaceomorphs do not show this condition and it is likely that the erinaceomorph P^3 is primitively a simple, small, and somewhat triangular tooth as in *Diacodon* and *Scenopagus* (Novacek, 1982). Most erinaceids, certainly Recent ones, retain this latter condition, but at least two early members of the family show the derived sespedectine trait of a large P^3 that is closely similar to P^4. Resemblance is most striking with *Galerix socialis* from the Miocene of Europe (see Engesser, 1972, p. 44). However, this genus departs from sespedectines in having the characteristic erinaceid features noted above and in table 7.

Another putative galericine, *Tupaiodon* Matthew and Granger (1924) from the Oligocene Hsanda Gol Formation of Mongolia (see Butler, 1948), bears a close similarity to sespedectines in the P^3, P^4 condition. In addition, the Asian genus departs from typical erinaceids and resembles sespedectines in having a small, premolariform upper canine and a very small or absent paraconule on M^{1-3}. *Tupaiodon* does, however, show characteristic erinaceid traits lacking in sespedectines. Closer comparison with the original material is warranted.

As for other early galericines, the case for close relationships with sespedectines seems, if anything, weaker than for the abovementioned candidates. Other species of *Galerix* (including *Pseudogalerix*) have a very small P^3 (see Engesser, 1972). *Tetracus* (early Oligocene, Europe) is poorly known but appears to have a double-rooted P_2 not notably small-

er than P$_3$ (Butler, 1948; Saban, 1958). *Lanthanotherium* (middle–late Miocene, Europe; late Miocene–early Pliocene, North America) has a more specialized dentition seen in galericines (two lingual roots on M$^{1-3}$ and a swollen posteriorly expressed hypocone in M^3). Although the metaconule is swollen in *Lanthanotherium* in a manner similar to that in *Sespedectes,* not all sespedectines share this trait. It seems likely that the character was independently derived in the two genera. *Neurogymnurus* (late Eocene–middle Oligocene, Europe) has large double-rooted canines and anterior premolars, a small triangular P^3, and several of the diagnostic dental traits of erinaceids.

From the discussion above, it is clear that most of the "evidence" for the alleged affinity between sespedectines and early galericines resides in primitive resemblance. Only the well-developed P^3 in *Galerix socialis* and *Tupaiodon* and the inflated metaconule in *Lanthanotherium* suggest special relationships.

Other subfamilies of erinaceids fail to show special traits that link them with sespedectines. Brachyericines have greatly enlarged lower incisors, shortened face, reduced P$_4$ trigonid, greatly elongated shearing crest on P^4, and very small M$_2$ that seem to be more specialized expressions of the basic erinaceid condition (see Rich, 1981). *Amphechinus* (early Oligocene–late Miocene, Europe; late Oligocene–early Miocene, Asia; Miocene, Africa; late Miocene, North America) basically differs from sespedectines in the features it shares with other erinaceines (table 7). *Palaeoscaptor* (Oligocene, Asia) is dentally more primitive than *Amphechinus,* but shows that even early members of the Erinaceinae are easily distinguished.

A final comparison of sespedectines with putative erinaceids concerns *Proterix* Matthew (1903). As the name implies, *Proterixoides* was originally allied with *Proterix* by Stock (1935), and Butler (1948) and others supported his argument. McKenna and Simpson (1959) remarked, for example, that *Proterixoides* was near to the structural ancestry of *Proterix.* The latter genus is, however, peculiar in many dental and cranial traits and its relationships within the Erinaceomorpha remain uncertain (Rich, 1981).

Proterix resembles sespedectines primarily in the lack of specializations of molars and premolars characteristic of erinaceids — namely the lack of a marked M$_1$ prevallid and a progressive, posterior reduction in size of the lower molars; and the presence of a less developed "cutting" crest (metacrista) on the P^4, smaller paraconids on the lower molars, and smaller, less isolated hypocones.

Proterix does, however, seem more conservative than sespedectines in having a large, double-rooted upper canine, a small, triangular-shaped P^3, and a weaker metaconule on M^1. It seems more derived in the greatly shortened snout, the loss of P$_1^1$, the loss or aberrant structure of P$_2^2$, a more distinct hypocone on P^4, more quadrate molars, and the lack of hypoconulids on M$_{2-3}$. Only the bunodont morphology of the molar cusps and the small, single-rooted P$_2$ suggest a special relationship between sespedectines and *Proterix.*

These comparisons leave unresolved the problem of affinities of *Proterix.* The genus does not fit well within the Erinaceidae, and it should perhaps be formally excluded from that group (Rich, 1981, p. 109). *Proterix* may be related to sespedectines (though not to *Proterixoides* specifically), but it does not share many of the dental specializations that define that subfamily. It may, alternatively, be a close relative of "amphilemurids." Resemblances to brachyericines in tooth reduction and skull shape seem independently derived.

The dental evidence reviewed above does not support the allocation of the subfamily Sespedectinae to the Erinaceidae. The simplification and reduction in size of the anterior premolars is a departure from the basic condition in erinaceids. This departure is also characteristic of specialized dormaaliids (see Novacek, 1982). The bunodont construction of the molars is most like *Proterix,* a genus whose assignment to the Erinaceidae is equally suspect. The large, complex P^3 is matched only by the galericines *Galerix socialis* and *Tupaiodon.* Most importantly, sespedectines lack many of the important specializations of the dentition that define more "modern" erinaceids. These characters are present, though less developed, in the late Paleocene, early Eocene members of the group (e.g., *Litolestes, Cedrocherus, Entomolestes,* see Krishtalka,

TABLE 7

Comparative Dental Characteristics in Sespedectines and other Erinaceomorphs

a, primitive state; b, c, . . . n, more derived states. Presence of three or more states does not necessarily imply a morphocline (e.g., a–b–c). ?, Character unknown.

Characters	*Sespedectes*	*Crypholestes*	*Proterixoides*	*Dormaalius*	*Macrocranion*	*Gesneropithex*	*Amphilemur*	*Pholidocercus*	*Alsaticopithecus*	*Scenopagus*	*Ankylodon*	*Talpavus*	*Talpavoides*	*Diacodon*	*Mckennatherium*	*Litocherus*	*Diacocherus*	*Cedrocherus*	*Litolestes*	*Leipsanolestes*	*Entomolestes*	*Adapisorex*	*Neomatronella*	*Eolestes*	*Dartonius*	Galericinae	Erinaceinae	Brachyericinae
1. (a) P_1, P_2, P_3 present; (b) P_1, P_3 absent; (c) P_1, P_2, P_3 absent.	a	a	a^1	a^1	a	?	a	a	a	a	a	?	?	a	a^1	a	a	?	a	?	a	?	?	?	a	a	b	c
2. (a) P_2 moderate size, double-rooted; (b) P_2 small, procumbent, or peglike, single-rooted; (c) P_2 absent.	b	b^1	b	b	b	?	b	b	b	b	b	?	?	a	a	a	a^1	?	a	?	b	?	?	?	?	a	a	c
3. (a) P_3 moderately large, double-rooted; (b) P_3 small, procumbent, or peglike, single-rooted; (c) P_3 absent.	a	a	a	b	b	?	b	b	b	a	a	?	?	a	a	a	a	?	a	?	b^2	b^2	?	?	?	a	c	c
4. (a) P_4 with elongate talonid, talonid basin; distinct cusps; (b) P_4 with short bicuspid or unicuspid heel.	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	a	a	?	b	a	b	a	a	b	a	b	b
5. M_{1-2} (a) subequal in size; (b) moderate; or (c) marked progressive reduction in size from M_1 through M_3.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c	c	b	c	b	b	b	b	c	c	c
6. (a) M_1 trigonids semi-compressed, paraconid crestiform, or lophid; (b) moderate; or (c) marked elongation of prevallid shear on M_1, paraconid crestiform or connate.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	b	b	b	b	b	b	c	c	c
7. Lower molar exodaenodonty (a) absent; (b) present.	b	b	b	a	a	b	b	b	b	a	a	a	a	a	a	a	a	a	b	b	b	b	b	b	b	b	b	b
8. M_{1-3} trigonids (a) taller, erect; (b) lower, canted.	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	b	b	b	b	b	b	b	b	b	b	b
9. Distinct ectocingulum on labial M_{2-3} (a) absent; (b) present.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	a	a	a	a	b?	a	b	b	b
10. Hypoconids on M_{1-2} (a) moderate size; (b) small.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	b	b	b	b	b	b	b	b	b
11. Molar cusps (a) connate or sectorial; (b) slightly swollen; (c) very swollen, bulbous or bunodont.	c	b	c	a	a	c	c	c	c	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a

TABLE 7—(*Continued*)

Characters	*Sespedectes*	*Crypholestes*	*Proterixoides*	*Dormaalius*	*Macrocranion*	*Gesneropithex*	*Amphilemur*	*Pholidocercus*	*Alsaticopithecus*	*Scenopagus*	*Ankylodon*	*Talpavus*	*Talpavoides*	*Diacodon*	*Mckennatherium*	*Litocherus*	*Diacocherus*	*Cedrocherus*	*Litolestes*	*Leipsanolestes*	*Entomolestes*	*Adapisorex*	*Neomatronella*	*Eolestes*	*Dartonius*	Galericinae	Erinaceinae	Brachyericinae
12. P^2 (a) caniniform, two-rooted; (b) peglike, one-rooted; (c) absent.	b	b	b[1]	?	b	?	?	b	b	b	?	?	?	a	?	?	?	?	a[3]	?	?	?	?	?	?	a[3]	a[3]	c
13. P^3 (a) small to moderate triangular, at least two-rooted; (b) very small, peglike, or triangular; (c) large with several cusps, similar to P^4.	c	c	c	?	b	?	?	b	b	a	a	?	?	a	?	a	a	?	a	?	?	?	?	?	?	a[4]	b	b
14. P^4 hypocone (a) absent, very weak; (b) large, distinct.	a[5]	a[5]	a[5]	?	a	?	?	a	a	b	b	?	?	b	?	a	a[5]	?	a[5]	?	?	a[5]	a[5]	?	?	b	b	b
15. P^4 metacone (a) absent; (b) present.	a	a	a	?	a	?	?	a	a	a	b	?	?	b	?	a	b	?	a	?	?	b	b	?	?	a	a	a
16. M^{1-2} hypocones (a) small; (b) larger; (c) larger and situated posterolingually.	b	b	b	?	b	b	b	b	b	c	c	?	?	a	?	b	a	?	b	?	?	b	b	?	?	b	b	b
17. M^{1-2} stylar spurs (a) moderately developed; (b) weak or absent; (c) very prominent.	a	a	a	?	a	b	b	b	a	c	a	?	?	a	?	a	a	?	a	?	?	b	b	?	?	a	a	a
18. M^{1-2} (a) semirectangular; (b) subquadrate; (c) semiquadrate.	a	a	a	?	a	b	b	c	b	a	a	?	?	a	?	a	a	?	b	?	?	b	b	?	?	c	c	c
19. M^{1-2} hypoconid crest (a) absent; (b) present.	a	a	a	?	a	a	a	a	a	a	a	?	?	a	?	a	a	?	a	?	?	a	a	?	?	b	b	b
20. M^3 (a) transverse, semitriangular with distinct parastylar spur, hypocone weak or absent; (b) heart-shaped, weak or absent parastyle and hypocone; (c) transversely oval, hypocone; (d) posteriorly expanded, usually with enlarged hypocone; (e) M^3 absent.	a	a	b	?	a	?	?	b	b	?	a	?	?	a	?	a	a	?	?	?	?	b	a	?	?	d[6]	c	e

[1] Inferred from alveoli and partial or isolated teeth.

[2] Tooth small, but double-rooted.

[3] P^2 small, but connate and double-rooted.

[4] *Galerix* shows (secondary) enlargement of P^3.

[5] Hypocone vestigial or easily worn but posterolingual ("hypoconal") cingulum distinct.

[6] Greatly expanded with large hypocone in most galericines, but not in *Galerix*.

1976; Bown and Schankler, 1982; Novacek, 1982; Gingerich, 1983; Novacek, Bown, and Schankler, 1985).

The other candidates for relationship to the sespedectines belong to a group traditionally dubbed the Adapisoricidae. The nominal
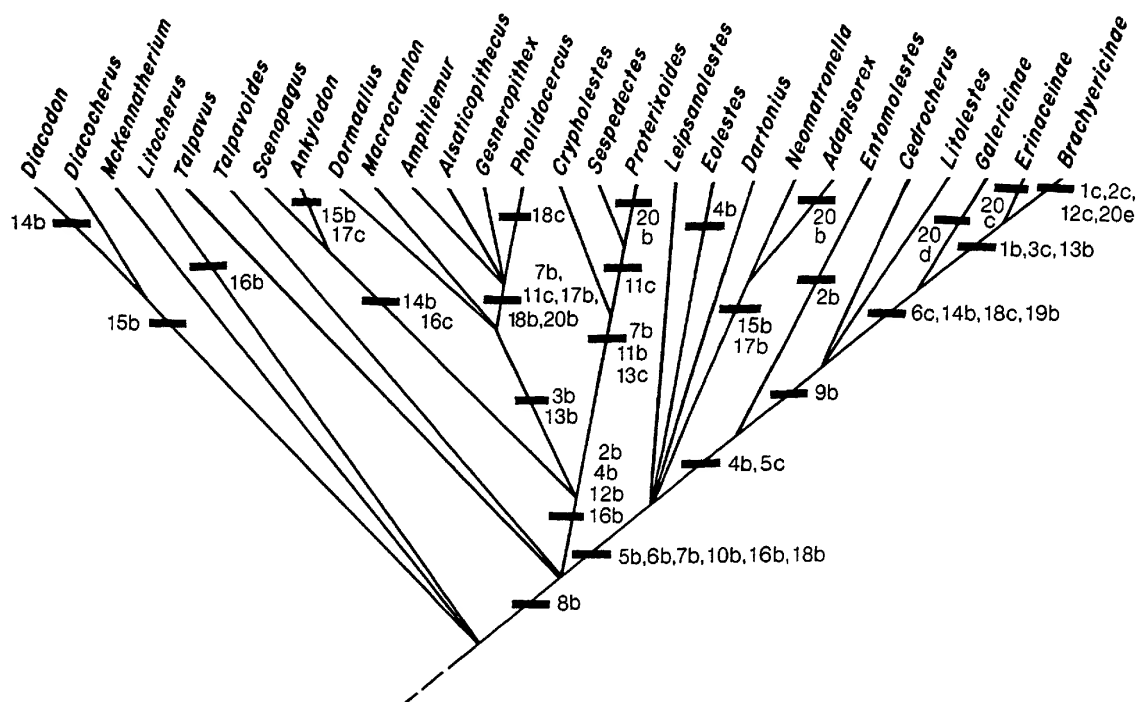
FIG. 9. Cladogram for erinaceomorphs. Numbers represent derived characters described in table 7.

taxon for this group, *Adapisorex*, is, however, more likely a member of the Erinaceidae (Krishtalka, 1976; Novacek, Bown, and Schankler, 1985). Typical "adapisorids" differ markedly from *Adapisorex*. A recent proposal is the recognition of two specialized erinaceomorph families in addition to the Erinaceidae (Novacek, Bown, and Schankler, 1985). These are the Amphilemuridae and the Dormaaliidae (see also Koenigswald and Storch, 1983). Several erinaceomorphs whose generalized dental condition precludes their assignment to the foregoing families (e.g., *Diacodon*, *Adunator*, *Diacocherus*, and *Litocherus*) are regarded as Erinaceomorpha *incertae sedis* (Novacek, Bown, and Schankler, 1985; table 1).

Table 7 summarizes comparisons of sespedectines with a variety of erinaceomorphs, including "amphilemurids," dormaaliids, and early, more dentally conservative, members of the Erinaceidae. Arguments for homologies and polarities of most of these dental characters are presented in Novacek (1982). Unlike more primitive *incertae sedis* taxa (e.g., *Diacodon*), sespedectines have small P_{1-2} with single roots and simplified crowns;

P_4 with short, simple talonids; at least an incipient hypocone on P^4; lower, more canted trigonids on M_{1-3}; and reduced, crestiform to lophid paraconids. These characters support the affinity of sespedectines with dormaaliids and "amphilemurids." This is reflected in the scheme of relationships portrayed in a cladogram (fig. 9).

Within dormaaliids, sespedectines show somewhat closer resemblance with *Dormaalius* and *Macrocranion* than with the *Scenopagus-Ankylodon* grouping. Like the former, but unlike the latter, P_{1-2}^{1-2} are more reduced (P_{1-2} are poorly known in *Scenopagus*) and the lower molar trigonids are less erect. Like *Macrocranion*, but unlike *Scenopagus* and *Ankylodon*, the upper molars of sespedectines are more quadrate (upper molars are unknown in *Dormaalius*). However, these differences are subtle and the relevant characters are unknown in some critical taxa. It seems best to recognize sespedectines, the *Scenopagus-Ankylodon* group, and the *Dormaalius-Macrocranion* group as three separate clades within Dormaaliidae.

The remaining possibility—that sespedectines are more closely related to "amphilem-

urids"—is even more difficult to assess. The crucial dental evidence is lacking in some referred "amphilemurids." At present, the preferred organization of the character evidence is reflected in the cladogram (fig. 9). Although the bunodont crown pattern is strikingly similar in *Sespedectes, Proterixoides,* and "amphilemurids," this condition is not comparably developed in the sespedectine *Crypholestes.* To retain the integrity of the sespedectines based on specializations of the P^3–P^4 condition (fig. 3; table 7) requires the independent development of the bunodont condition in amphilemurids and sespedectines. Moreover, the reduced, single-rooted P_3, and more quadrate upper molars in "amphilemurids" are more closely matched by *Macrocranion,* suggesting a close affinity between these taxa. Discoveries of more developed P_3s in certain "amphilemurids" where this tooth is presently unknown (e.g., *Gesneropithex*) would weaken this hypothesis.

If the scheme of relationships portrayed in figure 9 is accepted, it would certainly not be reflected in a family-level rank for the Amphilemuridae. A phylogenetic classification that better represents the higher-level branching in the cladogram would take the following form:

Order Insectivora
   Suborder Erinaceomorpha
      Superfamily Dormaaleoidea
         Talpavus
         Talpavoides
        Family Dormaaliidae
          Subfamily Scenopaginae
            Scenopagus
            Ankylodon
          Subfamily Dormaaliinae
            Dormaalius
            Macrocranion
          Tribe Amphilemurini
            Amphilemur
            Gesneropithex
            Alsaticopithecus
            Pholidocercus
         Subfamily Sespedectinae
           Crypholestes
          Tribe Sespedectini
            Sespedectes
            Proterixoides

Superfamily Erinaceoidea
   Erinaceoidea *incertae sedis*
      Eolestes
      Dartonius
      Neomatronella
      Adapisorex
      Leipsanolestes
   Family Erinaceidae
      Entomolestes
      Cedrocherus
      Litolestes
     Subfamily Galericinae (see Butler, 1948)
     Subfamily Brachyericinae (see Rich, 1981)
     Subfamily Erinaceinae (see Butler, 1948; Rich, 1981)
Erinaceomorpha *incertae sedis*
     Diacodon
     Diacocherus
     Mckennatherium = Adunator
     Litocherus

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